paratype of *umbratica* in Pasadena. Mr. C. B. Perkins and Mr. C. G. Abbott have made useful suggestions with respect to the manuscript.

KEY TO THE SUBSPECIES OF CHARINA BOTTAE

A. Scale rows 45 or more; parietal usually divided .... *bottae*
AA. Scale rows 44 or less; parietal usually entire
  B. Ventrals more than 191; posterior edge of frontal sharply angular or semicircular; sharp point of supraocular penetrating to some depth between frontal and parietal .... *utahensis*
  BB. Ventrals less than 192; posterior edge of frontal only slightly convex; supraocular with blunt end, penetrating little between frontal and parietal .... *umbratica*

SUMMARY

The rubber snakes may be divided into three subspecies, *Charina bottae bottae* of the Pacific Slope, *C. b. utahensis* of the Great Basin, and *C. b. umbratica* in southern California. The numbers of scale rows and ventrals are the best key characters for segregating these subspecies.

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TRANSACTIONS

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THE SIDEWINDER, CROTALUS CERASTES, WITH DESCRIPTION OF A NEW SUBSPECIES

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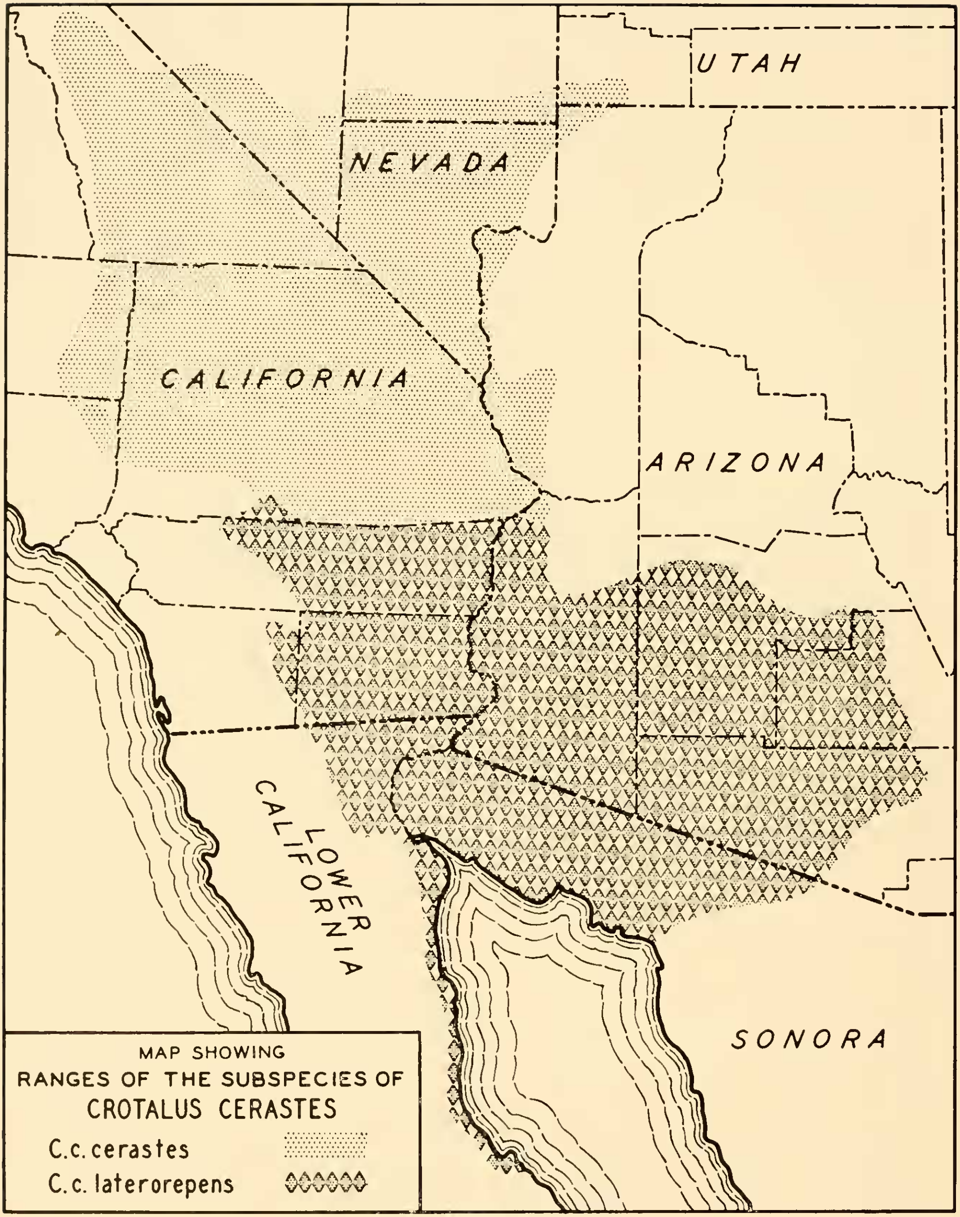
UTAH
NEVADA
CALIFORNIA
ARIZONA
LOWER CALIFORNIA
SONORA
MAP SHOWING
RANGES OF THE SUBSPECIES OF
CROTALUS CERASTES
C.c. cerastes
C.c. laterorepens

THE SIDEWINDER, CROTALUS CERASTES, WITH DESCRIPTION OF A NEW SUBSPECIES

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Introduction

The sidewinder, or horned rattlesnake, is one of the most characteristic animals of our southwestern deserts. While by no means restricted to sandy areas, its peculiar method of progression, a sort of flowing sideways, is particularly adapted to traversing such a yielding medium as sand.

Color differences between sidewinders from diverse areas have been often noted—there seems no doubt that they tend to resemble the hue of the sand or soil on which they live, varying through shades of cream, tan, pink, light-brown, and gray. In addition to these color modifications, certain differences in lepidosis and pattern, between the sidewinders of the Mojave and Colorado deserts, have been observed. In fact, there is no difficulty in distinguishing adult specimens, and most juveniles, from the two particular areas of these deserts which contain the most characteristic variants, but the allocation of specimens from other areas is not so clear-cut. I am of the opinion, however, that the recognition of a Colorado Desert subspecies is warranted.

The type locality of *C. cerastes* is given by Hallowell (1854) in this rather indefinite way: "Borders of the Mohave river, and in the desert of the Mohave . . . The river of the Mohave spreads itself out in the desert and there loses itself, and upon the floating sand hills near it these animals are found." Whether the type specimen is still in existence is not known, although there is some possibility that it may be Acad. Nat. Sci. Phila. No. 7098. In fact, there is, in this case, no certainty that the type specimen was collected at the stated type locality, the situation being analogous to that so frequently existing between Say's type specimens and the observations relating to the position of Long's Expedition when similar specimens were said to have been seen. At any rate, the description of the type leaves little doubt that it was a juvenile female and that it came from the Mojave Desert, and quite likely from near the river, but just where along the river is not known.

A NEW SUBSPECIES FROM THE COLORADO DESERT

In order to illustrate the differences between the snakes of the two deserts, I propose to compare two series, one from the region of the Mojave River at the middle of its course—for adequate specimens are unavailable from around the sink—and the other from the immediate vicinity of the type locality of the new subspecies. With these as bases, I shall then indicate the variations and allocations of the inhabitants of other districts. Since the paratype series of the new subspecies is of greater interest than a single specimen, I shall condense the description of the holotype. The new subspecies may be known as

Crotalus cerastes laterorepens subsp. nov.

COLORADO DESERT SIDEWINDER

Plate 5, fig. 2.

Type.—No. 34074 in the collection of LMK, collected at The Narrows, San Diego County, California, at 7:45 p.m., June 6, 1941, by C. B. Perkins and Charles E. Shaw. Preserved June 13, 1941.

Diagnosis.—A subspecies of *Crotalus cerastes* differing from the typical form of the Mojave Desert in having 23 rather than 21 scale rows, a higher number of ventrals, and a black instead of a brown proximal lobe of the rattle-matrix. Other differences of morphology and pattern are discussed hereafter.

Description of the Type.—An adult male. Length over-all (before setting in preservative) 604 mm.; length of tail 51 mm. The head length is 27 mm. The rattle string comprises 8 segments and is incomplete. The width of the proximal rattle is 7.8 mm. The scale rows are 25-23-18; all rows except the lowest on either side are keeled; the mid-dorsal row exhibits conspicuous tubercles or bosses, which are also present, but somewhat reduced, on the next row on each side; they are most evident at mid-body. There are 12 scale rows around the middle of the tail. The ventrals number 148 and the subcaudals 23, most of them being entire. The anal is undivided. There are 13-13 supralabials, and 14-14 infralabials. The rostral is wider than high; it is contacted by six scales: a first supralabial and prenasal on each side, and a pair of internasals. There are three canthals on each side between the internasals and supraoculars. The other scales on top of the head are highly irregular, and are rugose; there are about 24 scales anterior to the supraoculars. The minimum intersupraoculars are 5+5. The nasals are divided below, but not above, the posterior section being the larger. The loreals are 1-1; the preoculars 2-2, the upper being the larger; the post- and suboculars number 6-6. There are three rows of scales on each side between the supralabials and the orbit. The supraoculars are extended into prominent horn-like but flexible processes, jutting above and beyond the eyes. The head scales in the parietal region are tubercular, becoming keeled and forming regular rows toward the neck.

The head is buff above, but is given a grayish cast by the presence of many punctations, which are especially concentrated on the snout. There is a postocular dark stripe of punctated gray-brown on either side, which terminates above the last supralabial. There is a prominent light cross-dash on each supraocular, narrowing outwardly and edged with a fine black line. In the parietal region there are 4 large and several smaller spots of gray-brown edged with darker. Below, the mental and first three infralabials are punctated; otherwise the lower surface of the head is unmarked.

The body is ivory or buff dorsally but is given a grayish cast by the presence of many dark punctations. On the body there is a longitudinal series of 38 major dorsal blotches of yellow-brown, emphasized by many darker punctations. These are about 2½ scales long by 5 scale rows wide, and are quite irregular in shape. They are partly edged with black. The centers of these blotches were yellow in life. The dorsal punctations are somewhat less evident, both within and between blotches, on the central row. Laterally there are smaller secondary blotches, irregular both in size and shape; there are 4 series of these, the lowest of which engages the outer edges of the ventral scutes, which otherwise are immaculate. All of these side blotches consist of concentrations of punctations, often restricted to a single scale. On the tail there are 5 or 6 irregular cross-marks, the first brown, the others black. These black tail marks are conspicuously the darkest maculations on the snake. There are some irregular black marks on the underside of the tail. The proximal rattle-matrix lobe is black, as seen through the rattle, while the second lobe is black anteriorly.

Summary of Paratypes.—As paratypes I have used 95 specimens of *laterorepens* from the Borego area of San Diego County. Most of these were collected along the road from the foot of Sentenac Canyon to the San Diego-Imperial County line, 3 miles east of Benson's Dry Lake, a distance of 20½ miles. This road passes through The Narrows. A few are from the Borego Valley, north of The Narrows, while some are from the now-abandoned San Felipe townsite to the southeast; but all are from within a radius of 13 miles of The Narrows, the type locality of this subspecies. These specimens are LMK 1762, 1858, 2209–10, 4571–2, 4645–7, 4827, 4875, 4931, 4958, 5052–5, 5173–5, 9507, 21098, 21426, 22275, 22357, 23009, 23233, 23640, 23858, 23860, 23917, 23954–6, 23998, 24006, 24019–20, 25423, 25445, 26729–31, 26823, 26847–8, 26857, 26865–6, 26937–8, 27240, 28113, 28228, 28682–3, 28728, 28750, 29085, 29118–9, 29271, 29277, 29898, 30719, 31930, 31999, 32307, 32977–8, 33044, 33058–9, 33123, 33333–5, 33342, 34035, 34176–9, 34351, 34570, 35179, 35187–8, 35305, 35557–9, 35597, 35634–5.

The statistics of the principal countable characters in the paratype series (including the holotype itself) are set forth in Table 1. These will be discussed later in pointing out salient differences between the Borego *laterorepens* and Mojave *cerastes*.

As to the patterns in this series of paratypes, they have almost universally a grayish or clay-colored cast. The ground color is in reality buff or ivory, but the dorsums are much speckled with brown or dark-gray. The youngest specimens are often the grayest.

The dorsal blotches are usually evident, but are obsolescent in some specimens, although not to the extent characteristic of certain other areas. The dorsal blotches may be dark-gray, or light-brown, but retain little or none of the yellow characteristic of these specimens in life. The same is true of the postocular dark streak. The mid-dorsum is usually less punctated than other areas of the back. The dorsal blotches are often irregularly outlined in black. The lateral secondary blotches are fairly distinct in some specimens, but are highly irregular and indefinite in others. When most distinct they comprise single scales, heavily punctated with dark-brown or even black. The edges of the ventrals are usually punctated. Head markings (except the postocular dark streaks) are highly irregular, and often absent; however, light supraocular cross-marks are generally present. Except in the juveniles, black tail marks are conspicuously evident; these are rather irregular in arrangement, seldom being in the form of even rings.

In a series of live specimens from the Borego area the following colors were found, using the designations of Ridgway, 1912. The ground color is Light Buff to Pearl Gray, heavily punctated with Brownish Olive dots. The postocular streaks are Honey Yellow to Isabella Color, as are also the centers of the dorsal blotches. The ventrum is White to Marguerite Yellow. The posterior tail rings are Black. It was noted, when these specimens were preserved in alcohol, that the yellow almost disappeared. Also, there seems little doubt that the colors of live sidewinders are somewhat affected by temperature in the manner so much more evident in lizards.

Comparison of Subspecies.—For purposes of comparison with the type series of the new subspecies, I have taken a series of 107 specimens of *cerastes cerastes* from the desert plains surrounding the middle Mojave River. These comprise the best available series from anywhere in the vicinity of the indefinite type locality, given as the "Borders of the Mohave river and in the desert of the Mohave." I have used them as a sort of informal type series. Most of the specimens comprising this lot were collected along highway U. S. 395 in the 30 miles between Adelanto and Kramer Junction, San Bernardino County, California. There are also scattered representatives from along U. S. 66 as far east as Daggett, Minneola, and Newberry; from westward at Lovejoy, Piute, and Pinnacle buttes in northeastern Los Angeles County; and from Muroc Dry Lake in southeastern Kern County. All of the area thus included comprises but a small part of the Mojave Desert—a part contiguous to the middle stretch of the Mojave River.

The major countable characters of these two type series are compared in Table 1. Out of 12 characters (9 independent) 8 are found to be significantly different in the two areas, employing the usual level of $P=0.05$. But significance—that is, the real existence of a difference not chargeable to

TABLE 1

Statistics of Typical Series of Sidewinders

Character	Mojave *cerastes*					Borego *laterorepens*					Differences	
	N	ER	IR	M	V	N	ER	IR	M	V	CD	P
Scale rows	107	19 – 23	20.79 – 21.66	21.22∓.06	3.06	96	21 – 25	22.18 – 23.44	22.81∓.10	4.10	7.21	.0001—
Ventrals male	78	132–143	135.22–138.55	136.89∓.28	1.80	58	140–149	143.50–146.43	144.97∓.29	1.50	5.74	.0001—
female	29	136–146	139.04–142.34	140.69∓.46	1.74	38	143–154	146.58–150.21	148.40∓.44	1.81	5.34	.0001—
Subcaudals male	78	20 – 26	21.37 – 23.04	22.21∓.14	5.59	58	20 – 24	21.07 – 22.66	21.86∓.15	5.38	— 1.56	.104
female	29	15 – 19	16.28 – 17.65	16.97∓.18	6.00	38	15 – 19	16.39 – 17.98	17.18∓.19	6.89	1.28	.429
Supralabials	213	11 – 14	11.96 – 12.87	12.41∓.05	5.47	191	11 – 14	11.99 – 13.08	12.53∓.06	6.49	0.97	.106
Infralabials	213	11 – 15	12.24 – 13.39	12.82∓.06	6.65	191	11 – 15	12.47 – 13.72	13.10∓.07	7.07	2.18	.0015
Scales between supralabials	104	2 – 5	3.32 – 4.30	3.81∓.07	19.08	94	2 – 7	3.74 – 4.84	4.29∓.08	18.94	11.86	.0001—
Body blotches	107	30 – 43	34.25 – 37.94	36.09∓.26	7.58	96	32 – 44	35.50 – 38.89	37.20∓.26	6.75	3.02	.004
Tail rings male	78	3 – 6	4.05 – 5.11	4.58∓.09	17.10	58	4 – 6	4.31 – 5.35	4.83∓.10	16.08	5.34	.065
female	29	2 – 5	3.02 – 3.95	3.48∓.13	19.76	38	3 – 5	3.52 – 4.43	3.97∓.11	17.03	13.17	.005
Width of button, mm./10	49	27 – 33	29.19 – 31.43	30.31∓.24	5.48	52	31 – 38	33.14 – 35.78	34.46∓.27	5.67	12.83	.0001—

EXPLANATION: N, number of counts; ER, extreme range; IR, interquartile range; M, mean with standard error; V, coefficient of variation in per cent; CD, coefficient of divergence between subspecific means in per cent; P, significance of difference computed by the null method. A positive value of CD indicates that *laterorepens* is higher than *cerastes*.

the exigencies of sampling—is not to be accepted as the sole criterion of relative importance. We must also take into consideration the extent of differences, as measured by the coefficient of divergence, and the nature of the characters involved. I consider the subcaudals, and more especially the tail rings, as of minor importance since neither is determinable with high accuracy—the subcaudals because of the feathering at the rattle, and the tail rings because of the irregularity of these marks. The latter, however, while not important numerically, are of importance from the standpoint of color.

If we take the characters which are both significant and involve a coefficient of divergence exceeding 5 per cent, we have scale rows, ventral scutes, scales between the supraoculars, tail rings of the females, and the width of the button. These are important and definite differences, although not equally valuable as key characters. Tables 2 and 3 give the arrays of the first two. Although overlapping is evident, the important extent of the differences will be clearly seen.

As estimates of the overlapping in the ventral scale counts of these series of *cerastes* and *laterorepens*, we may use the criterion of the standard range, as suggested by Simpson (1941) and Simpson and Roe (1942). This is the estimated range that a sample of 1000 specimens would have, and is determined by multiplying the optimum estimate of the standard deviation of the population by 3.2414 and adding the result to, and subtracting it from, the mean. The standard ranges of the ventrals thus computed are as follows:

	MALES	FEMALES
Cerastes	128.90 to 144.88	132.75 to 148.63
Laterorepens	137.94 to 152.00	139.69 to 157.11

The percentage of overlapping of the populations may be determined by a formula suggested in a previous paper (Klauber, 1943, p. 56). The results are 4.0 per cent for the males and 6.7 per cent for the females. The actual overlaps, in my relatively small samples, are 4.4 per cent in the males and 9.0 per cent in the females.

The divergence in the size of the button (Table 1) is an indication of a body-size difference between the two subspecies, for the button constitutes a residual record closely correlated with body size just after birth. This difference is further validated by the maximum sizes found in the two type series, as follows:

	MALES	FEMALES
Cerastes	555 mm.	583 mm.
Laterorepens	660 mm.	767 mm.

Cerastes is the only rattlesnake known in which the females consistently exceed the males in size.

TABLE 2

Distribution of Scale Rows in the Type Series

Scale Rows	Mojave *cerastes*	Borego *laterorepens*
19	1	
20		
21	90	14
22	6	5
23	10	67
24		5
25		5
Total	107	96

TABLE 3

Distribution of Ventral Scutes in the Type Series

Ventral Scutes	MALES *cerastes*	MALES *laterorepens*	FEMALES *cerastes*	FEMALES *laterorepens*
132	4			
133	4			
134	6			
135	6			
136	12		1	
137	15		2	
138	13		2	
139	8		5	
140	4	1	4	
141	3	2	4	
142	2	5	5	
143	1	9	2	2
144		5	2	2
145		12	1	2
146		10	1	2
147		5		6
148		7		3
149		2		9
150				3
151				5
152				2
153				1
154				1
	78	58	29	38

The following color notes were made on live specimens from the two areas:

	Mojave *cerastes*	Borego *laterorepens*
Ground color	Fawn to light-brown	Ivory to tan
Punctations	Smaller and less evident	Heavy and conspicuous
Dorsal blotches and postocular dark streak	Red-brown to dark-brown, sharply outlined	Yellow to brownish-olive, indefinitely outlined
Proximal matrix-lobe in adults	Red-brown to dark-brown	Black

The last-named item comprises one of the most easily applied and consistent key characters wherewith to distinguish the two subspecies; unfortunately, it is not applicable to the juveniles, for the black color of *laterorepens* does not become fully evident until the acquisition of the third or fourth rattle at the earliest, and is sometimes not present until the seventh or eighth rattle is attained. It should be understood that this criterion refers to the rattle-matrix itself, as seen through the rattle, and not to the last dark marks on the tail, although these also are usually red-brown or dark-brown in *cerastes* and black in *laterorepens*. The lateral areas of the matrix are more important than the top and bottom, which are often blotched with light, even in adult *laterorepens*.

Segregation of Subspecies

Although the proper classification of individuals from the two type areas involves little or no difficulty, this is not true of some other areas, partly because the material at hand is somewhat inadequate, but mostly since the subspecific differences are not so consistent or sharply drawn. As is usually the case, the characters are not modified simultaneously; in the present instance the two easiest-applied key characters—number of scale rows and color of proximal rattle-lobe—are not always transformed coincidently.

The material available comprises some six hundred specimens distributed as shown in Table 4.

The areas most poorly represented are the eastern portions of Riverside and San Bernardino counties, in California; some parts of Arizona (particularly Mohave and northern Yuma counties); and Sonora. This situation is the result of a lack of collecting activities rather than the rarity of the snakes, which are, in fact, quite common in some districts from which few or no specimens are available in study collections.

TABLE 4

Localities of Specimens of *Crotalus cerastes* Available for Study

State	*County*	*Number of Specimens*
California	San Diego	125
	Imperial	53
	Riverside	88
	San Bernardino	99
	Los Angeles	48
	Kern	15
	Inyo	26
	Mono	1
Nevada	Nye	9
	Clark	20
Utah	Washington	17
Arizona	Yuma	34
	Mohave	1
	Maricopa	27
	Pinal	12
	Pima	7
Sonora		2
Lower California		11
Uncertain		34
		629

Using the number of scale rows and ventrals, and the color of the proximal rattle-matrix as guides, a considerable part of the range of the sidewinder may be allocated to one subspecies or the other on the combined trends of all three characters. The areas thus assigned are as follows:

To *cerastes*	To *laterorepens*
Western San Bernardino County	Lower California
Los Angeles County	San Diego County
Kern County	Imperial County
Inyo County	Yuma County
Mono County	West-central Riverside County
Nye County	
Clark County	

It should be understood that the listing of a county in this tabulation does not indicate that sidewinders are found throughout the county; the tabulation refers only to the section in which they occur. For example, *cerastes* inhabits only the extreme northeastern corner of Los Angeles County.

The segregations thus made account for about two-thirds of the sidewinder's range. The decisions with respect to the rest of the area involve determinations based on inadequate material, or upon giving pre-eminence to one differential character as compared to the others. With regard to the latter, I have decided to make the color of the basal lobe of the rattle-matrix the primary criterion, not because I deem it more important than scale rows or ventrals, but because, by its use, there is less subspecific overlapping, and the identification of single specimens is made more simple and direct. However, it must be re-emphasized that it is applicable only to fully grown adults. Further, occasional deviations are to be expected in any territory. For example, a specimen of *c. cerastes* from near Furnace Creek Inn, Death Valley, has a black matrix, as have several snakes from the islands in Lake Mead.

Upon this basis we can make the following additional allocations:

Washington County, Utah: Assigned to *cerastes* based on 21 scale rows and matrix color; the ventrals are intermediate, being somewhat higher than in typical *cerastes.*

Eastern San Bernardino County, California, and *Mohave County, Arizona:* Assigned to *cerastes.* All characters justify this allocation, but the material is inadequate for a final determination.

Eastern Riverside County, California: Assigned to *laterorepens,* although specimens with 21 scale rows slightly outnumber those with 23. This makes the Riverside-San Bernardino line the approximate boundary in California between the two subspecies. Along this line intergradation is to be expected, as is suggested by specimens from Twentynine Palms and Blythe Junction (= Rice).

Arizona, east of Yuma County: Maricopa County seems quite certainly assignable to *laterorepens.* Pinal and Pima counties are likewise, on the criterion of matrix color, although both scale rows and ventrals are low for the southerly subspecies. As nearly as can be determined from two specimens, Sonora should also be considered *laterorepens* territory.

RANGES AND LOCALITY RECORDS

The ranges so determined may be summarized thus:

Cerastes: The desert regions of eastern (but not extreme southeastern) California, southern Nevada, southwestern Utah, and northwestern Arizona, including the following: extreme southern Mono, Inyo, eastern Kern, northeastern Los Angeles, and San Bernardino counties in California; southern Nye, extreme southern Lincoln, and Clark counties in Nevada; southwestern Washington County, Utah; and extreme northwestern, and west-central Mohave County, Arizona.

Laterorepens: The desert areas of central and eastern Riverside, northeastern San Diego, and Imperial counties in California; northeastern Lower

California, Mexico, from San Francisquito Bay north; northwestern Sonora, Mexico; and Yuma, Maricopa, Pinal, and Pima counties, Arizona.

The detailed locality records available are given in the lists below. These omit a number of doubtful localities, especially some given in the popular literature. The term "sidewinder" is rather widely used throughout the southwest as a designation for any small rattlesnake, and therefore it has been frequently reported from areas where its occurrence is quite impossible. For example, some accounts of the Hopi Snake Dance mention sidewinders as being used, whereas the snakes referred to are really *Crotalus viridis nuntius*.

CERASTES

California: *Mono County*—Chalfant; *Inyo County*—Laws, Bishop, Lone Pine, Alico Siding, Keeler (also 4 and 5 mi. se.), base Inyo Mountains (1 mi. s. of Keeler), 8 mi. ne. of Olancha, Cowan Station, Dunmovin, Linnie, Panamint Valley, Ballarat, Panamint Mountains (vic. Goler Wash), 4 mi. w. of Townes Pass, Mesquite Valley, also Mesquite Spring (n. end Death Valley), Stovepipe Wells (also 4 mi. sw. and 1 and 6 mi. e.), 7 mi. sw. of Boundary of Death Valley National Monument in Boundary Canyon, 1 mi. sw. of Hole-in-the-Rock Spring, Beatty Junction (12 mi. n. Furnace Creek Inn), Furnace Creek (also 6 mi. nw.), Furnace Creek Ranch, 3 mi. nw. of Borax Mines, Funeral Mountains (4 mi. s. of mouth of Echo Canyon), Echo Canyon, 1 mi. w. of Ryan, Bennetts Well, 10 mi. s. of Shoshone (on Cal. 127), 12 mi. n. of Trona (S.B.Co.), Borax Flats Water Station; *Kern County*—Brown (also 6 mi. e.), Leliter, China Lake, Inyokern (also 8 mi. s. and 8 mi. se.), 1 mi. nw. of Freeman Junction, Terese, Randsburg (also 2 mi. n.), Red Rock Canyon, Cinco, Neuralia, Mojave (also 5 mi. n. and 5 mi. e.), Boron (= Amargo) (also 3 and 4 mi. w.), Muroc, Muroc Dry Lake (= Rogers Dry Lake) (also n. end of lake); *Los Angeles County*—15 mi. e. of Lancaster (also 22, 24, and 28 mi. se.), Piute Butte, Pinnacle Butte, Lovejoy Buttes, Lovejoy Springs, Peck's Butte (also 1 and 2 mi. s.), Wilsonia, 8 and 9 mi. e. of Llano; *San Bernardino County*—14 mi. e. of Inyokern, Borax Flat, Atolia (also 2 and 3 mi. s.), Kramer, Kramer Hills, Kramer Junction (also 3, 5, 6, and 7 mi. n.; 1 and 2 mi. e.; 1 mi. w.), Adelanto (sidewinders have been collected in every mile of the 30 miles between Kramer Junction and Adelanto), 2 and 4 mi. s. of Adelanto, 15 mi. e. of Wilsonia (L.A.Co.), Phelan, L. A. Co. line w. of Victorville, Victor Valley near Victorville, 6 and 12 mi. n. of Miller's Corner, Jimgrey (also 2 and 3 mi. e.), Hawes (also 2 mi. w.), Eads, Hinkley, Lenwood, Hodge, Wild, Helendale, Bryman, Oro Grande, Victorville (also 2 and 3 mi. e.), Hesperia, Lucerne Valley, Sidewinder Well, Stoddard Well, Ord Mountains, Coolgardie, Leach Spring, Bicycle Lake, Camp Irwin, Calico Mountains, Yermo, Cronise, Baker (also 32 mi. n.), Barstow (also 3 and 5 mi. ne., and 8 mi. s.), Nebo, Daggett (also 5 mi. e.), Gale, Minneola, Newberry Spring, Rancho Larga Vega, Troy (also 4 mi. e.), Hector, 3 mi. s. of Lavic, Ludlow, Siberia, 4 mi. e. of Bagdad, Rock Corral, 6 mi. e. of Lone Star, Twentynine Palms (also 8, 9, and 16 mi. w.), Blythe Junction (= Rice), 8 mi. w. of Clark Mountain, 3 mi. sw. of Kelso, Fenner, Goffs, Klinefelter, Needles.

NEVADA: *Nye County*—Sarcobatus Flat, North Amargosa, Amargosa Desert, 3 mi. w. and 18 mi. se. of Beatty, Death Valley National Monument Boundary at Highway 58, 15 mi. n. of Ash Meadows, Pahrump Valley; *Lincoln County*—Quartz Spring; *Clark County*—Indian Springs Valley, Indian Springs (also 2 mi. w.), Pahrump Valley, Vegas Valley, Las Vegas (also 16 and 22 mi. nw., and 6 mi. sw.), Erie, Dry Lake (RR Sta.), Glendale (also 1 and 3 mi. w., 3 mi. sw., 14 mi. e., 1 mi. n.), Lovell, near St. Joe (= bet. Glendale and Logandale), Mormon Mesa near Virgin River, Mesquite, Lower Muddy Valley, Atlatl Rock (Valley of Fire), 1 mi. s. of St. Thomas, Virgin Valley, Hemenway Wash, Islands in Lake Mead, 3 mi. above Boulder Dam, Boulder City, 1½ mi. nw. of Fort Mojave.

UTAH: *Washington County*—Beaver Dam, Beaver Dam Mountains, near Arizona State Line (on U.S. 91), St. George (also 5 mi. n.), Sugar Loaf (near St. George), Red Hill (n. of St. George), ½ mi. s. of Bloomington, 2 mi. w. of Indian Reservation Farm, Hurricane. (Alpine, Utah County, reported in the literature, is now considered inaccurate.)

ARIZONA: *Mohave County*—U. S. 91 just s. of Utah line, near Kingman, 1 mi. s. of Yucca, 6 mi. n. of Topoc.

LATEROREPENS

CALIFORNIA: *Riverside County*—2 and 5 mi. e. of Cabazon, Snow Creek, Snow Creek Hatchery, Whitewater (also 3 mi. se.), Palm Springs R.R. Station (also 1 and 3 mi. se., and 1 mi. nw.), Palm Springs (also 5 and 6 mi. nw., 4, 9, and 12 mi. se.), Cathedral City (also 1 and 2 mi. nw., 3 mi. s., and 3 mi. se.), 3 mi. s. junction of Cal. 74 and Cal. 111 (also 3 mi. w.), Indian Wells (also 4 and 6 mi. w.), La Quinta (also 1 mi. e.), Indio, Sand Hills (e. of Indio), Coachella (also 6 mi. s.), Torres, Oasis, Flying Sphinx Ranch (near Oasis), Mecca, Box Canyon (near Mecca), Myoma, Garnet (also 3 and 4 mi. n., and 5 mi. ne.), Edom, Little Morongo Canyon (Little San Bernardino Mountains), Wide Canyon (and 7 mi. nw.) (Little San Bernardino Mountains), Pushawalla Canyon (Little San Bernardino Mountains), Fargo Canyon (Little San Bernardino Mountains), Shaver Summit, Chuckwalla Mountains, Dos Palmas Valley (w. side), North Shore Road (Salton Sea), Salton, Hayfield, Desert Center (also 5 and 8 mi. e., and 5 and 17 mi. w.), Chuckwalla Valley, Hopkins Well (also 5 and 6 mi. w.), Blythe (also 17 mi. w. and 2 mi. e.), 2 mi. s. of Blythe Junction (San Bernardino County), near Neighbors; *San Diego County*—Beatty's Ranch (Borego Valley), De Anza Ranch (Borego Valley), Borego Springs, 6 mi. e. of Borego P.O. (also 2 and 5 mi. s.), 8 mi. ne. of The Narrows, Yaqui Well, The Narrows (type locality of *laterorepens*), Benson's Dry Lake, Imperial County line 3 mi. e. of Benson's Dry Lake, (sidewinders have been collected in every mile of the 20 miles from the foot of Sentenac Canyon via

Yaqui Well, The Narrows, and Benson's Dry Lake to the Imperial County line), San Felipe (abandoned townsite), La Puerta (= Mason Valley), Carrizo Spring (also 5 mi. nw.), Dos Cabezas; *Imperial County*—Fish Springs, Truckhaven, Arroyo Salada (at U.S. 99), Tule Wash (at U.S. 99), Arroyo Grande (at U.S. 99), Kane Spring (also 5, 10 and 12 mi. nw., and 4 and 5 mi. se. on U.S. 99), Kane Spring Junction (U.S. 99 and Cal. 78) (also 7 mi. w.), Trifolium, half way between Westmorland and Kane Spring, 5 and 8 mi. w. of Westmorland, Vendels, Echo Island (Salton Sea), Sandy Beach (Salton Sea), New River at Salton Sea, Myers Creek Bridge (U.S. 80), Ocotillo (= Millers), Painted Gorge (also 6 mi. sw.), 5 mi. s. of Coyote Mountain, Coyote Wells (also 2 and 5 mi. e. on U.S. 80, and 2 mi. w.), Yuha Plain (10 mi. s. of Coyote Wells), Petrified Forest (sw. cor. Yuha Plain), Plaster City, Dixieland (also 1 mi. w.), Seeley (also 16 mi. w.), Laguna Station (near present town of Seeley), 11 mi. w. of Imperial, Calexico, 4 mi. e. of Bond's Corner, Holtville (also 4, 6, 8, 10, 12, mi. e. on U.S. 80), Date City (also 10 mi. e.), Midway Well (Junction U.S. 80 and Cal. 98; also 2 mi. e. and 3, 4, and 6 mi. w.), Gray's Well (also 2, 4, and 6 mi. e. on U.S. 80), 10, 11, 14, 17, 18, 20, and 26 mi. w. of Yuma on U.S. 80, Ogilby Junction, Springers, 1 mi. w. of Little Valley Wells Maint. Station, Pilot Knob (also 6 mi. n.), 3 mi. n. of Bard, 3 mi. n. of Potholes, Araz, Andrade, Coyote Valley (se. corner of county), Black Hills.

LOWER CALIFORNIA: Nw. of Laguna Salada, Cocopah Mountains, e. base of Cocopah Mountains, Pattie Basin, San Felipe, San Felipe Bay, San Francisquito.

SONORA: Punta Peñasco, 9 mi. ne. of Punta Peñasco en route to Sonoyta. (Dr. Seth Benson states that he has seen sidewinder tracks at Kino Bay.)

ARIZONA: *Yuma County*—Kofa Mountains, Yuma (also 1 and 3 mi. s., and 5, 8, 10, 11, 15, and 25 mi. e.), Yuma Mesa, 5 mi. ne. of Somerton, ½ mi. n. of San Luis (Sonora), Monument 200 (15 mi. from Colorado River), Araby, Dublin, Ligurta, Welton (also 5 mi. w., and 17 and 19 mi. e.), Welton Mesa, Tacna, Pembroke, Kim, Mohawk (also 5 and 9 mi. e.), Mohawk Mountains (also e. base), Chrystoval (= Stoval), 1 mi. e. of Aztec, 25 mi. e. of Tule Tank; *Maricopa County*—Vulture, 1 mi. s. of Morristown, Coldwater (= 18 mi. w. of Phoenix), Agua Caliente, Gila Bend (also 10 and 28 mi. e., and 10 and 15 mi. s.), Maricopa Mountains (19 mi. e. of Gila Bend), Phoenix, Tempe, Salado Valley (near Tempe), Mesa (also 9, 10, and 12 mi. e., and 14 mi. ene.), Desert Wells, Stewart Mountain Dam; *Pinal County*—Foot of Superstition Mountain (23 mi. e. of Mesa), Sacaton, Casa Grande (also 5 mi. w.), Casa Grande National Monument, Coolidge (also 5 mi. e.), 3 mi. se. of Picacho, 8 mi. e. of Red Rock; *Pima County*—Growler Valley, Bates Well, Growler Pass (11 mi. sw. of Ajo), Ajo (also 6 mi. ne. and 20 mi. n.), 5 mi. ne. of Sells, Marana, Santa Cruz River (near Marana), Cortaro, 12 mi. n. of Tucson. (The following records are to be deemed doubtful without further confirmation: Fort Buchanan and Tubac, Santa Cruz County; and Tombstone, Cochise County.)

Intrasubspecific Color Variations

Having discussed the variations of the two subspecies, in determining to which the snakes of some areas should be allocated, I shall now comment upon less-important differences of color and pattern. Most of the color varieties of the sidewinder are localized, as shown by differences found within rather restricted areas.

One of the most clearly defined color phases occurs in the sand hills some 18 miles west of Yuma, and from these hills westward across the desert to the edge of the irrigated area of the Imperial Valley. These specimens of *laterorepens* are generally pink, with dorsal blotches almost obsolete; where present, the spots are burnt-orange in color. Dorsally these snakes are heavily punctated with brown dots, but superficially they appear almost unicolor, except for the conspicuous black tail rings. The blotches become obsolete only in the adults. Similar almost-patternless sidewinders are found to the west of the Imperial Valley, especially in the vicinity of Coyote Wells and Painted Gorge, where the same type of desert, characterized by sandy mesquite hummocks, occurs. Strangely enough, specimens of *c. cerastes* from the sand hills on the floor of Death Valley, between Stovepipe Wells and Furnace Creek, have the same characteristic loss of blotches. These Death Valley snakes are stunted, as indicated by the size of the proximal rattles when they have reached parallelism.

In southwestern Utah, and in nearby corners of Arizona and Nevada, most of the specimens are decidedly pink or reddish. The dorsal blotches are distinct. The postocular dark stripe is often extended into a hook around the commissure, or there may be a break, with an extra spot there. Thomas Rodgers informs me that a specimen from Atlatl Rock, Valley of Fire, Clark County, Nevada, which was found on sloping sandstone, was a beautiful pink in life.

The snakes of the Coachella Valley in Riverside County, are much like those from Borego Valley, in San Diego County—ash gray and much punctated. The black tail rings are broad and conspicuous, even more so than in the *laterorepens* paratypic series.

The most definitely marked snakes, with wide dorsal blotches clearly and evenly outlined, are from Nye County, Nevada, especially from the country lying northeast of Death Valley. Snakes from around Boulder Dam, as evidenced by those collected on the islands as the water rose in the reservoir, are also clearly marked.

Some specimens from around Yuma have obsolete blotches, similar to those from parts of Imperial County. Further southeast into Pima County they are tan or gray, with blotches moderately evident.

Of the two specimens from Sonora one is pink, the other gray. Miss Margaret Storey tells me that the specimen from Punta Peñasco had brilliant orange blotches in life.

The most southerly specimen from Lower California, that from San Francisquito, was probably tan in life, with fairly distinct spots. Its most notable character is the large size of the black tail blotches.

MORPHOLOGY

The largest specimens of *c. cerastes* that I have seen are: male, 555 mm.; female, 587 mm. A male measuring 628 mm. from intergrading territory has been noted. The smallest specimen (not including the broods mentioned elsewhere) was 171 mm. In *c. laterorepens* the largest male measured 665 mm., the largest female, 767 mm. The smallest measured 190 mm. Both minimum juveniles were collected in the fall.

The sidewinder is a stout-bodied snake, as compared to other rattlers. The weight-length curve (based largely on the subspecies *laterorepens*) was found to be approximately $W = 930\ L^{3.42}$, W being expressed in grams and L in meters (Klauber, 1937, p. 44). As the exponent is greater than 3, sidewinders get proportionately stouter as they age.

It is also a large-headed and broad-headed snake (Klauber, 1938, pp. 8, 38, and 48). Using the methods hitherto discussed, I have redetermined the head (H) to length over-all (L) regression lines separately for the subspecies *cerastes* and *laterorepens*, with the following results: for the Mojave series of *cerastes*, $H = 5.8 + 0.0368L$; and for the paratypic series of *laterorepens* $H = 6.0 + 0.0378L$. Both H and L are expressed in millimeters. There is little difference between these lines; they give the following head lengths at an assumed standard body length of 550 mm.; *cerastes* 26.0 mm.; *laterorepens* 26.8 mm. The coefficient of divergence at this body length is therefore 3.03 per cent, not an important difference. There is noted a tendency of some of the largest adult females of both subspecies to have larger heads than indicated by these equations. However, the positive value of the constant term in both equations indicates that juveniles have proportionately larger heads than adults, as is the case with most vertebrates.

The fangs of *c. cerastes* are proportionately shorter than those of *c. laterorepens*, as shown by the following average figures for 5 adults of each subspecies:

	L/F	H/F
Mojave *cerastes*	120	5.69
Borego *laterorepens*	98	4.83

Cerastes is found to have a somewhat shorter fang than would be expected from consideration of the usual relationship existing between subspecies having different adult sizes (Klauber, 1939a).

The palatine teeth in *laterorepens* are 3–3, the first being slightly smaller than the other two. The pterygoid teeth are 8–8 and are slightly shorter and heavier posteriorly. The dentary teeth are 8–8 or 9–9, also growing smaller posteriorly (scaphiodont).

The tail-length regression equations (see Klauber, 1943, p. 51), derived from the two type series, are as follows (both T and L being expressed in mm.):

Cerastes males	$T = -6.0 + 0.107L$
Laterorepens males	$T = -3.6 + 0.090L$
Cerastes females	$T = -0.2 + 0.065L$
Laterorepens females	$T = -0.5 + 0.063L$

It will be observed that there is a considerable ontogenetic change in the males, whose tails grow proportionately longer as they age; in the case of the females the constant term in the regression equations is too small to be important. The coefficients of divergence between the two subspecies at an assumed standard body length of 550 mm. are: males 14.1 per cent; females 4.0 per cent, *cerastes* having the longer tail. The male difference is undoubtedly significant. The respective coefficients of sexual dimorphism are: *cerastes* 39.1 per cent; *laterorepens* 29.4 per cent. This is a higher sexual difference than is found in most rattlesnakes.

Ecological Preferences

Sidewinders prefer the sandy areas of the desert, yet they are by no means restricted to sand, being often found in places where the surface is baked hard, and where stones are strewn about. But they do occur in the most extreme arenaceous areas and they are rare or absent on rocky hillsides where no soft ground is nearby. If the territory is diverse, sidewinders are more likely to be found in the flats, particularly about sand hummocks, or along sandy washes. For example, they are plentiful along the sandy wash of San Felipe Creek, from Yaqui Well to The Narrows and beyond; but up the rocky side-canyon of the Sentenac they have never been taken, although this territory has been hunted assiduously. Nor are they present in In-Ko-Pah Gorge, above the Myers Creek crossing on U.S. 80. But where they are able to follow washes and thus reach isolated valleys, they will persist there, as is the case in La Puerta Valley of eastern San Diego County. In flats of this kind they are by no means restricted to places where the soil is loose or sandy. I should say that the ideal territory for the sidewinder comprises desert flats with scattered brush, and where sand hummocks, crowned with mesquite, or sandy washes are prevalent. And they can exist in terrain which is entirely sand, as shown by their presence in the sand hills some 20 miles west of Yuma in Imperial County, where the strip of dunes is fully 5 miles wide.

The sidewinder seems to be driven out by irrigation, being absent in the cultivated sections of the Imperial Valley, where it was plentiful before 1900. The same is true of the area southwest of Yuma. I have found one *laterorepens* DOR at Date City, near Holtville, where both sides of the road were cultivated, but this was near a neglected field which had reverted to desert. The inability of the sidewinder to survive such an ecological change is in contrast with some other snakes, such as the desert gopher snake, *Pituophis catenifer deserticola*, which is now much commoner in the cultivated than in the primitive areas of the desert.[1]

Laterorepens is a lower-altitude subspecies than *cerastes;* I have no records much above 2000 feet. Without doubt it is found slightly higher at La Puerta, in San Diego County, and near Ajo and to the northwest of Tucson, in Pima County, Arizona. From these points it ranges down to below sea level around the Salton Sea. *Cerastes*, on the other hand, ranges from below sea level in Death Valley to at least 4500 feet in Sarcobatus Flat, Nye County, Nevada, and 4200 feet at Chalput, Mono County, and near Bishop, Inyo County, California. Much of the range of *cerastes*, particularly the western Mojave near the probable type locality, is at an altitude of about 2500 feet. Eventually the division between the two subspecies may be found to follow the contours of the eastern Mojave.

Where the sidewinder is thoroughly at home it is likely to be quite plentiful. In the western Mojave Desert in the Barstow-Kramer-Adelanto triangle, I judge it to be the commonest nocturnal snake, with the possible exception of *Arizona elegans occidentalis* and *Crotalus scutulatus*. In San Diego County, along the Yaqui Well-Narrows-Benson's Dry Lake road, it is the fourth commonest snake, being exceeded by *Phyllorhynchus decurtatus perkinsi*, *Sonora occipitalis annulata*, and *Arizona elegans occidentalis*.[2]

Conditions Governing Activity; Example Field Notes

Sidewinders are primarily nocturnal animals. As a proof one may cite the fact that in many thousands of miles of travel on the desert only one was found active on the highway in the daytime, while 129 were collected along the road at night. Yet, while their activities are essentially nocturnal, they are found abroad, but usually resting, in daylight, especially in the temperate sun of the early spring and the late fall, or early in the morning in the summer before the heat has become unbearable.

Some idea of the hours when sidewinders have been found on the road may be gained from the data of Table 5. While necessarily this table represents the hours of activity of the collector as well as his quarry, the gradual increase in numbers after twilight proves that *cerastes* is not primarily crepuscular. As to the later evening hours, while it is true that such hours are not as often used by us for hunting as the earlier evening, yet there have been many occasions when collecting obviously diminished as the ground cooled below the optimum temperature. So we may judge that when the most

[1] For frequency statistics see Klauber, 1939b, Table 12, p. 52.

[2] For detailed statistics see Klauber, 1939b, Table 18, p. 60.

favorable temperatures are experienced in the early evening, the snakes do go below ground later. Unfortunately, there having been little collecting in the hours just before dawn in the summer, we are unable to determine whether this is a time of activity, as might be expected from the fact that temperatures then would be most to the liking of the snakes.

TABLE 5

Time of Evening when Sidewinders have been found Active on Roads

Time	Subspecies *Cerastes*	Subspecies *Laterorepens*
6:30- 6:59	1	
7:00- 7:29	2	4
7:30- 7:59	9	10
8:00- 8:29	6	7
8:30- 8:59	9	10
9:00- 9:29	5	6
9:30- 9:59	9	16
10:00-10:29	2	5
10:30-10:59	3	4
11:00-11:29	1	3
11:30-11:59		1
	47	66

Table 6 shows the air temperatures at times when sidewinders have been found on the road at night. It indicates that these snakes, particularly of the subspecies *cerastes*, are not seriously affected by moderately low temperatures. The data of this table might be misunderstood in one particular. I do not think that *cerastes* deliberately seeks evenings of lower temperature than *laterorepens;* rather, the western Mojave, being at a higher altitude than the western Colorado desert, and less protected by adjacent mountains from the strong west winds of the spring evenings, *cerastes* finds it necessary, because of the requirements of food and mating, to be abroad under less favorable circumstances. At any rate, one is repeatedly surprised at the conditions which these snakes withstand; I have found them when the cold wind was so strong as literally to sweep them across the smooth surface of the highway. I judge their spring season of activity to be as early as that of any snake found on the desert, which is surprising since some of the other forms range into more temperate areas, and should thus be more accustomed to low temperatures, while the sidewinder is restricted to the desert. Of course, it is to be remembered that ground temperatures are even more important than air temperatures; there is evidence that under some conditions the snakes seek the highways because they have remained warmer than the adjacent sand.

TABLE 6

Air Temperatures at Times when Sidewinders have been found Active on Roads

Air Temperature Degrees Fahr.	Subspecies *Cerastes*	*Laterorepens*
62	4	
64	3	
66	3	2
68	2	1
70	3	
72	5	
74	1	2
76	3	11
78	1	5
80	2	8
82	1	
84		2
86		3
88		9
90		1
92		
94		1
96		1
98		1
	28	47

The season of greatest activity is from the last week in April to mid-June. Thus May is the most productive single month. The season probably lags from one to two weeks in the higher altitudes.[3]

Certain features of sidewinder activities may be best described by citing a few typical incidents.

On April 25, 1932, near Glendale, Nevada, two *c. cerastes* were caught on the road at 7:45 and 8:25 p.m., with a strong, cold wind blowing; and another snake, probably of the same species, escaped. This occurred before temperatures were recorded, but I suspect it was well below 60° F.

May 30, 1932: In the afternoon a small specimen was uncovered just below the surface of the sand dunes 18 miles west of Yuma. The head may have been above ground, but at least it was not seen by my son, who found it.

April 19, 1936: At about 9 o'clock in the morning, I found a large sidewinder by following its track. This was at the eastern edge of the sand hills, 14 miles west of Yuma. The snake was stretched out, quite inactive, in the

[3] For statistics on a snakes-per-mile-of-travel basis see Klauber, 1939b, Table 7, p. 46.

shade of a creosote bush. A year later (May 2, 1937) a large female (length 730 mm.) was found in the same locality; this was at 8:30 a.m. This snake was at the foot of a mesquite, about 18 inches from the entrance to a hole, and with head and neck resting in a hollow in the mesquite trunk. The snake was entirely in the shade. It was warm, with little wind.

In the evening of the same day, I had a sidewinder come directly at me in his best fighting pose. As I stepped out of the way his purpose was clear—he was seeking refuge under the car. This is an example of how stories of rattlers attacking people may start. Parenthetically, it may be said that among people living in the desert, sidewinders are reputed to be both pugnacious and very poisonous. As to the first, I have not found them conspicuously different from other rattlers; as to the second, Githens and George (1931), and Githens (1935) place *cerastes* in an intermediate position in the scale of rattlesnake venoms from the standpoint of virulence. Since the sidewinder is a relatively small snake, and the venom is not exceptional, it is less dangerous than its larger congeners. With regard to venom yield, I can report that 169 sidewinders, about half of which were adults, produced an average of 22.8 milligrams of dried venom per snake. Several small groups of adults averaged from 40 to 50 milligrams, and two sets averaged 65.8 and 68.4 respectively. It is evident that in exceptional cases secretions of at least 80 milligrams must be reached. This compares with yields of from 100 to 300 milligrams in the larger species of rattlesnakes, and even exceeding 1000 in exceptional cases (Klauber, 1936a, p. 209).

September 4, 1937: A small sidewinder bit itself while being captured. It was dead next day—the only one of a number of snakes caught at this time which did not survive the trip.

September 25, 1938: James Deuel found at the foot of Borego Mountain, a *Lampropeltis getulus californiae* (ringed phase), which was eating a *laterorepens* head first. When released the sidewinder seemed uninjured.

June 1, 1940: This evening at 8:30 a *laterorepens* was found in Pushawalla Wash, Little San Bernardino Mountains, Riverside County, coiled in the sand beside the road. The temperature was 80°F. The snake had scooped out a little hollow so that its back was even with the surface of the ground. This is a quite characteristic method used by the sidewinders, for they are frequently found in the daytime, flush with the ground surface (see Gloyd, 1937, p. 124, for illustration), if the temperature is moderate.

On April 24, 1943, James Deuel found a sidewinder 3 miles northeast of Barstow; it was neatly coiled in the sand, exposed to the sun, at 9:10 a.m., and was reluctant to move, until disturbed with a stick.

Collecting

There are several methods of collecting sidewinders, such as driving on desert paved roads at night, hunting around sand dunes with a flashlight, or tracking snakes in the early morning. The latter method was preferred by several professional collectors whom I interviewed. It was their practice to start out at daylight, either among mesquite hummocks or along the bank of a sandy wash, particularly where there were sand slides. Of course, they were searching for any snakes, but particularly the rattlers *C. cinereous*, *C. scutulatus*, and *C. cerastes*, sidewinders being often found in association with one or both of these. An early start is necessary for two reasons: to find the tracks before they have been obliterated by the morning wind, and to come upon the snakes before they have sought refuge in holes. It is the custom of the snakes to lie about the holes or on the edges of the brush for a part of the morning, the time depending on the season and the advent of an uncomfortable degree of heat. In fact, in the early spring and late fall *cerastes* may spend much time above ground, either coiled in the sand, in a hollow scooped out for the purpose, or stretched out under the protection of a bush. I have been told by experienced collectors that nearly every track results in a capture by this method, and that a territory continuously worked will soon become depleted of snakes.

In the early days of my own collecting, I hunted at night in sand dunes with a flashlight. This is not a particularly fruitful method, as the snakes' cryptic coloration makes them difficult to see among the twigs and desert debris. This scheme was therefore soon superseded by the method of driving along paved desert roads at night, picking up the snakes found crossing the road in the glare of the headlights of the car. Because of the large area covered, and the fact that, under certain temperature conditions, the snakes stay on the road to profit from the warmth retained in the pavement, this is a much more prolific scheme than the older one. Full details of this method and its results will be found elsewhere (Klauber, 1939b).

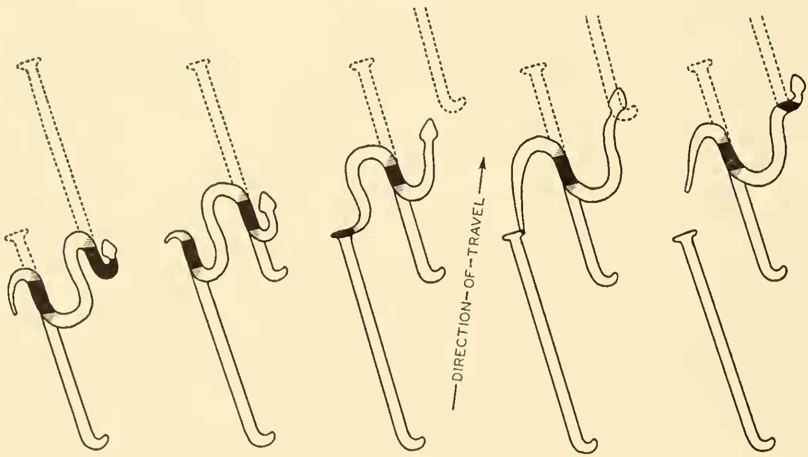
LOCOMOTION

The peculiar method of locomotion of the sidewinder, which gives the snake its name, is a side-flowing or looping motion whereby only vertical forces (rather than transverse) are applied to the supporting surface. The track comprises a series of short and separated lines, set at an angle of about 30 deg. with the direction of progression, each line approximating the length of the snake. If the track be in fine sand, and undisturbed by wind, the impressions of the ventral scutes can be clearly seen, for there is no transverse or sliding motion. Each section of the track has a fairly evident *J*-shaped mark (made by the head and neck) at one end, and a *T*-shaped terminus (made by the tail) at the other. The direction of progression, if one desires to track the snake, is that toward which the hook of the *J* is pointing; however, the *T*-shaped mark left by the tail is nearer to the destination than the *J* made by the head.

All snakes tend to sidewind, if placed on a smooth or very yielding surface, but, of course, they are not as adept as a sidewinder, which uses the same motion even on a firm surface, although he can use a more normal method if he wishes. It is said that the viper *Cerastes* of the Sahara Desert has developed a motion quite similar to that of this rattlesnake.

The sidewinding motion, although it appears clumsy, not only facilitates movement across a soft medium, but is relatively speedy. I think a sidewinder can travel as rapidly, if not more so, than any other rattlesnake.

To describe the motion of the sidewinder analytically, it is necessary to segregate several elements of motion which the snake executes simultaneously. Assume a snake outstretched on the ground, with the body lying at an angle of about 30 deg. with the projected line of travel, but with the tail, rather than the head, pointing obliquely toward the objective. Using the central part of the body as an anchor, the head is projected forward in such a way that the



TEXT FIG. 1. Showing consecutive position of the snake's body in relation to the tracks. The solid track-outlines have already been made; the dotted outlines are yet to be made. Only the solid-black sections of the snake's body are in contact with the ground; the rest of the body is raised sufficiently to clear the ground. (After Mosauer, with modifications.)

anterior third of the snake makes an angle of about 60 deg. with the rest of the body; in so doing the head and neck form an angle of 30 deg. with the line of progression, but on the opposite side of the line from the angle made by the body. In advancing the head and neck they do not touch the ground until they reach a new anchorage point, although they are raised so slightly that one must have the eye close to the ground to note the clearance. Now the head and an inch or so of neck are brought into contact with the ground and serve as a new anchor, and from this anchor the snake lays out his body forward toward the objective—not directly toward it, but at an angle of 30 deg. As the body is being laid out, with the tail toward the objective, there is a sharp crook at the neck so that the stationary head faces in the direction of progression, although the body is being advanced further in that direction than the head itself. Then again the head reaches forward for a new anchorage and again the body is laid out in advance of it. But always in transferring from one anchorage to the next, whatever part of the body is in transition is raised slightly above the ground, so that the surface offers no resistance to this part of the movement, and no track is made; tracks are left only where the body is laid down obliquely in advance of the head. By this means virtually no transverse forces are applied to the supporting medium; only vertical forces are exerted, and the track is not a sinuous line, but a series of separate short straight lines, advancing in echelon toward the destination. Each section of track has a length equal to that of the snake; and, as only vertical forces are applied, with no sliding, the imprints of each ventral scale are to be seen in the sand (Plate 6).

Primarily, sidewinding represents the most efficient use of a loose supporting medium, such as sand, which can offer little resistance, and therefore little reaction, to transverse forces directed across the surface (as do the sticks, stones, and irregularities of ordinary firm ground by which the normal snake aids his sinuous progression), but can exert a considerable resistance to forces applied vertically.

A person watching a sidewinder will see no resemblance between the motion as I have described it—throwing out the head, laying down the body, throwing out the head again, etc.,—and what the snake seems to be doing; for, as I have said, the snake telescopes these operations by executing several simultaneously. Long before the tail has been placed, at the end of the laying down sequence, the head has already reached out for a new anchorage, so that the moving snake is never, even for an instant, fully outstretched along any one of his tracks. As a matter of fact, he is always touching at least two tracks at once, with that portion of his body between tracks slightly clearing the ground surface; and at the time the head is first touching its next anchorage, the tail-tip is just leaving the track two steps behind, so that for a moment the snake may actually contact three tracks at once.

From the standpoint of step-by-step analysis, this is an accurate statement of what the snake does, but from a pictorial standpoint, it could hardly be worse. A sidewinding snake may best be described as one with a loose S-curve in his body; as the curves undulate the body appears to flow smoothly (and with a most unexpected rapidity) sidewise across the sand. Why the motion is said to be sideways is this: if a line be drawn from the snake's head to his tail and this be considered the snake's axis (although he is not outstretched, but in an S-curve), the line of motion will be seen to be perpendicular to this axis. In ordinary sinuous snake-motion it will be remembered that the progression is in the direction of an imaginary axis from tail to head. But a sidewinder goes sideways as compared to the direction that a normal snake having the same S-curve would take—hence "sidewinding."

For an excellent discussion of the details of sidewinding, including a description of the muscles employed, attention is directed to the papers by the late Dr. Walter Mosauer (especially 1930, 1932b, and 1935a).

The sidewinder is rounded rather than sharply angled at the line of the abdomen. Some species which normally inhabit sandy areas—*Sonora occipitalis* and *Chilomeniscus cinctus*, for example—have a definite angle along the edge of the ventrals, which serves as a boundary of the abdominal crawling surface, but this the sidewinder lacks.

Food

Sidewinders feed primarily on mammals (*Dipodomys* and *Perognathus* particularly) and lizards (especially *Cnemidophorus* and *Uma*). There is evidence that lizards are preferred by the young snakes, and mammals by the adults. This is shown by the following table:

	Cerastes		*Laterorepens*	
	Mammals	Lizards	Mammals	Lizards
Specimens containing food	11	5	13	10
Mean size of snakes, mm.	467	403	457	341
Limiting sizes, mm.	345-587	299-503	324-606	260-543

The preference of the younger snakes for lizards probably results from the greater prevalence of small lizards which the little sidewinders can successfully engulf, as compared with young mammals. The fact that the two lizards most often found in sidewinder stomachs—whiptails and fringe-footed sand lizards—are primarily diurnal, suggests that the snakes must often find their prey in holes. However, H. T. Woodall found a sidewinder eating a whiptail at mid-day above ground. This was at Twentynine Palms, in June. One *Cnemidophorus* removed from a sidewinder stomach showed a fang mark on its head. *Uta stansburiana stejnegeri* is another lizard which is eaten, and Van Denburgh (1922) reports one having swallowed a horned toad (*Phrynosoma platyrhinos platyrhinos*). I have been surprised to find no *Coleonyx variegatus* in sidewinder stomachs, although this gecko is common almost everywhere the rattlesnake occurs and is nocturnal. Possibly the soft-bodied geckos would only remain recognizable for a short time.

One sidewinder (a DOR, length 530 mm.) was found to contain a bird a California Yellow Warbler (*Dendroica aestiva brewsteri*). Another had swallowed a caterpillar, but as it also contained a *Uma*, it is possible it may have secured the lizard while the latter was eating the caterpillar. C. B. Perkins, at the San Diego Zoo, feeds adult sidewinders a full grown mouse, at intervals of a week or 10 days.

Reproduction

Sidewinders usually mate in the spring. However, fall matings do occur, as reported by Lowe (1942). A fall mating in captivity was also observed at the San Diego Zoo, Oct. 21, 1938.

J. R. Slevin found a pair of *c. cerastes* mating under a bush near Barstow at about 5 o'clock in the afternoon, during the last week in April. The male measured 425 mm., the female 530.

I have found two mating pairs of *laterorepens*. The first was on April 21, 1935, in mesquite sand hills one mile east of La Quinta, Riverside County. This was at 9 a.m. on a clear warm day. They were found by tracking. The snakes were lying quietly on the top of a dune in the shade of a bush. The tracks showed that there had been considerable joint activity nearby. The snakes were caught in a net with as little disturbance as possible and were placed in a wooden box with a hinged cover. Thereafter during the day (which was spent in alternate traveling and hunting) they were examined at approximately hourly intervals. They were beginning to separate, although still in copulation, at 4:25 p.m., and were fully separated sometime before 6 p.m. The left hemipenis of the male was used. The male measured 596 mm.; the female was 663 mm. in length and very stout-bodied.

The second pair was found at 8:50 p.m., May 6, 1939, on a branch road up Fargo Canyon, Little San Bernardino Mountains, Riverside County. There was a strong cold wind blowing up the canyon; evidently they had sought the warmth of the pavement. Although carefully placed in a box they were separated when we reached Indio at 9:20. The male measured 543 and the female 578 mm.

A *c. cerastes* from Piute Butte, Los Angeles County, gave birth to 10 young Oct. 15, 1939. The mother measured 542 mm.; the young 161 to 169 mm., with a mean of 166 mm. A *laterorepens* from Borego Valley, San Diego County, was brought to the San Diego Zoo May 15, 1937, and gave birth to 6 young Nov. 4, 1937. The young shed on Nov. 11. They varied in length from 176 to 187 mm.; mean 182 mm. A brood of 7 born to a mother said to have been taken in Riverside County, measured from 165 to 183 mm.; mean 176 mm. Another brood of 5 from a mother of uncertain origin measured 172 to 189 mm.; mean 179 mm.; date of birth Nov. 28, 1942. A sixth born dead, was only 152 mm. long. It is believed that natural births in the wild occur in the early fall; about Sept. 10 to Oct. 1, judging from the first appearance of young in the field.

Gravid females of *cerastes* have been noted to measure from 469 mm. to 560 mm., and of *laterorepens* from 434 mm. to 663 mm. The following numbers of eggs have been noted: *cerastes* 7, 8, 10, 10, 12, 13; *laterorepens* 6, 7, 8, 8, 11, 16.

As is usually the case with the rattlers (Klauber, 1936b, p. 8) the males seem to range abroad more than the females, particularly in the spring, so that they generally exceed the females in collections, although the actual populations are probably little, if any, unbalanced. For example, on an evening drive April 21, 1940, along the Adelanto-Kramer Junction road, 6 sidewinders were collected, all males, 5 adults and one adolescent.

The hemipenes are bilobed, with divided sulcus. The lobes are spinous at the base and frilled distally, terminating in calyculate apices. There is a sharp division between the spinous and frilled areas. The spines are rather short and heavy, reaching their largest size on the outer shoulders, where they form a conspicuous patch. They decrease in size by degrees around the edges of the patch, to tiny points, which renders an accurate count impossible. However, there are few small spines in the centers of the patches, differing in this respect from *viridis*. On the side opposite the sulcus the spines on each lobe extend to a second patch in the crotch. The spines per lobe vary in number from about 45 to 75, depending somewhat on how many of the little points are deemed large enough to be considered true spines. About 60 per cent are on the shoulders, the balance in the crotch or in the line between. Occasionally this mesial patch is almost completely separated from that on the shoulder. Compared with other rattlesnakes the spines are of medium length and rather heavy.

The frills or fringes are reticulate, rather than laminate, and have papillose edges. They number from 15 to 21 on each lobe.

The lobes have a length about 1½ times their thickness.

The male organs of *c. cerastes* closely resemble those of *laterorepens*. The lobes of the former appear to be proportionately somewhat slimmer, with a few more fringes and a few less spines.

In the proportionate size of the mesial patch of spines, *cerastes* is most like *pricei* and *willardi*. *Adamanteus* and *enyo* have more spines in this area; all other rattlers fewer. In the *viridis* group they are usually absent entirely. In having reticulated, rather than laminated fringes, *cerastes* is like *durissus*, *molossus*, *adamanteus*, and *tigris*. In the ratio of lobe length to thickness, *cerastes* (especially the subspecies *laterorepens*), is like *molossus* and *enyo*, most other rattlers having proportionately slimmer lobes. On the whole, except for the reticulated fringes, *cerastes* appears to resemble *enyo* most closely.

RELATIONSHIPS

The species *Crotalus cerastes* is rather sharply differentiated from all other rattlesnakes, not only because of the horn-like supraocular, but in its method of progression, and in the superiority of the females in size. In hemipenial characters it seems closest to *enyo*, and this is the case also in the prominent tubercles of the mid-dorsal scales. Thus we might be disposed to consider it as allied to the *durissus* group; however, it differs from the members of that group in having a proportionately large, and especially a broad, head, a short tail, and in the growth-equation of the rattle. In these characters, and likewise in the occasional scales between rostral and prenasal, it resembles *mitchellii*; yet *cerastes* has a relatively small rattle, proportionate to body size, while *mitchellii* is at the other extreme. Thus, while it seems to be nearest to *enyo* and the *mitchellii* group, it differs conspicuously from both.

Coues (1875) considered the sidewinder sufficiently different from other rattlesnakes, by reason of the horn and the roughness of the head scales, to warrant placing it in a separate subgenus *Aechmophrys*. This distinction is not recognized by modern herpetologists.

KEY TO THE SUBSPECIES OF *Crotalus cerastes*

Proximal lobe of rattle-matrix brown in adults; scale rows usually 21; ventrals in males 141 or less, and in females 144 or less *C. c. cerastes*

Proximal lobe of rattle-matrix black in adults; scale rows usually 23; ventrals exceed 141 in males, and 144 in females *C. c. laterorepens*

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SUMMARY

A new subspecies of the sidewinder or horned rattlesnake, *Crotalus cerastes* Hallowell, 1854, is described as *C. c. laterorepens*. This occurs in the desert regions of southeastern California (Riverside County and southward), northeastern Lower California, northeastern Sonora, and southwestern Arizona. The

typical subspecies, *C. c. cerastes*, is found in the Mojave Desert of California from southern San Bernardino County north to southern Mono County; and in southern Nevada, southwestern Utah, and northwestern Arizona. The differences between the subspecies entail scale counts, pattern, and color. Intrasubspecific differences are pointed out. Life history notes are presented.

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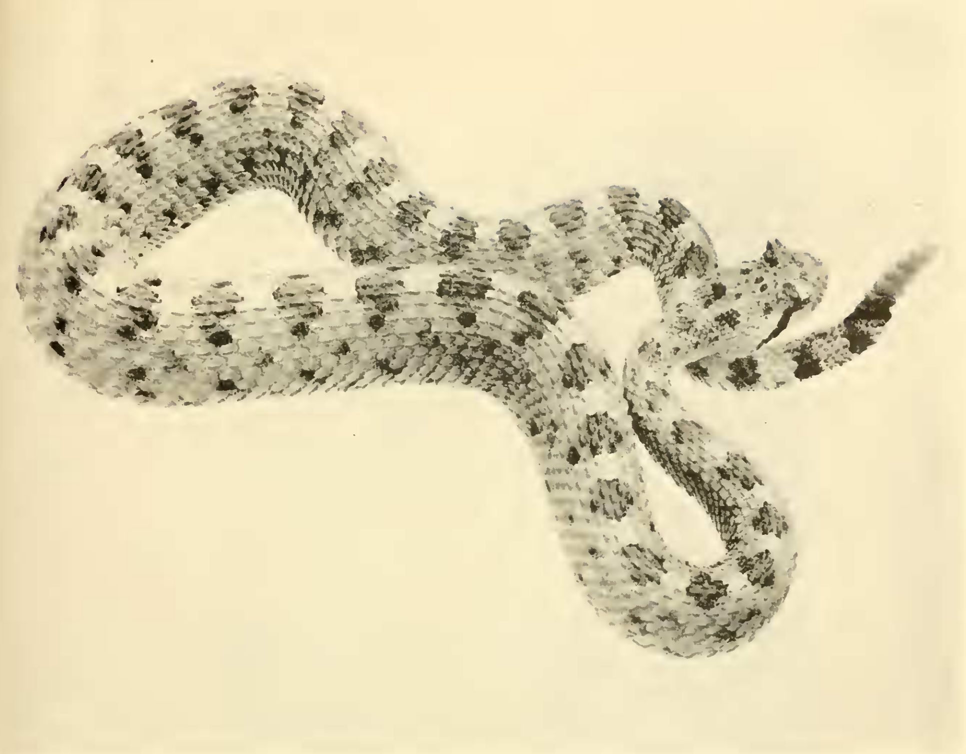

FIG. 1. *Crotalus cerastes cerastes.*
Adult male from 2 miles south of Kramer Junction, San Bernardino County, California.

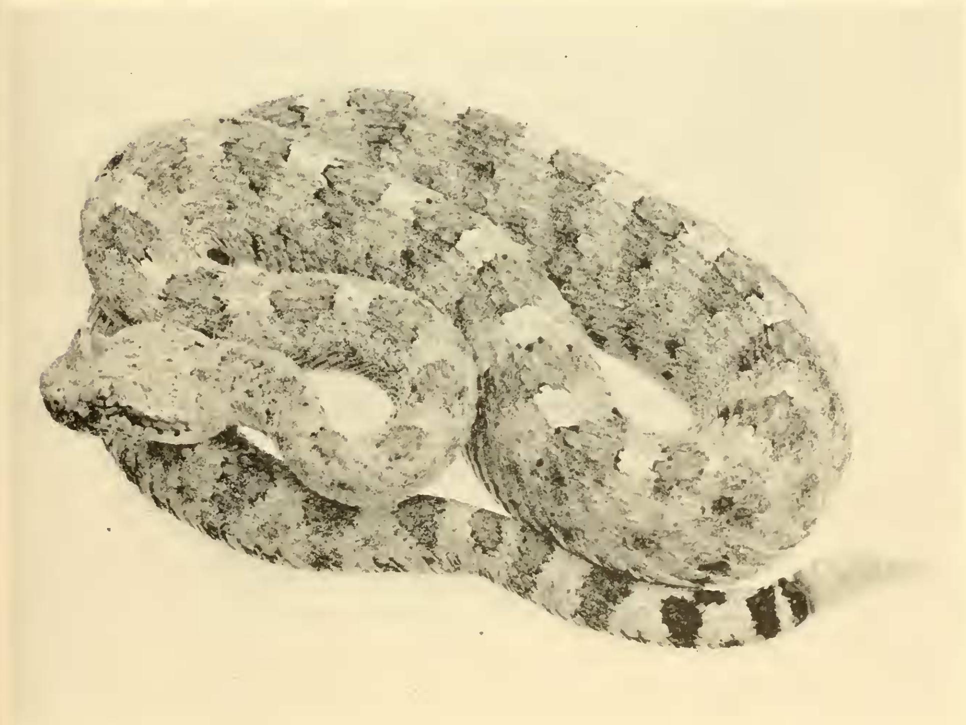

FIG. 2. *Crotalus cerastes laterorepens.*
Adult male from Borego Valley, San Diego County, California.

The track of an adult sidewinder traveling from left to right. The lower marks (rather less J-shaped than usual) were made by the head; the upper marks by the tail. The small tracks were made by beetles.

(Photograph taken in the sand dunes at Sandy Beach, Salton Sea Wild Life Refuge, Imperial County, California, by Dr. Raymond B. Cowles.)